

A DEVELOPMENTAL STUDY OF DUMORTIERA HIRSUTA
(SW.) NEES.

By PAUL M. PATTERSON

A DISSERTATION SUBMITTED TO THE BOARD OF UNIVERSITY STUDIES OF
THE JOHNS HOPKINS UNIVERSITY IN CONFORMITY WITH THE
REQUIREMENTS FOR THE DEGREE OF DOCTOR OF
PHILOSOPHY

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PLATES 4-8

INTRODUCTION

Fruiting *Dumortiera hirsuta* was found on the bank of a small stream in a ravine with a northern exposure, in a beech-oak woods near Columbia, S. C. Since no detailed study has been made of the development and cytology of this form, and since this genus is typically a tropical and sub-tropical one and therefore inaccessible to most botanists, it was thought that a study of the development of *Dumortiera hirsuta* would be of interest, both for itself and for comparison with other members of the *Marchantiaceae*.

Good descriptions of the gross morphology of *Dumortiera* including the structure of the thallus, surface, rhizoids, ventral scales and receptacles are available from several sources: e.g., Nees von Esenbeck (18), Leitgeb (37), Goebel (24), Engler and Prantl (15), Ernst (17), and others. A good account of the geographical distribution of this genus is given by Evans (20) and Herzog (32).

Evans (20) lists all the *Dumortieras* described under two species: *D. hirsuta* (Sw.) Nees. and *D. nepalensis* (Tayl.) Nees. This arrangement is given also by Evans (19) in his description of *Dumortiera* in the North American Flora where *D. trichocephala* Hook, *D. velutina* Schiffn., and *D. calcicola* Campbell are considered synonyms of *D. nepalensis* (Tayl.) Nees. Campbell (9) describes the development of antheridia in *D. velutina*, and of archegonia in *D. trichocephala* as being typically marchantiaceous. The earlier development in the embryogeny of *D. velutina* is given and a general account of the later development is discussed for both species. Ernst (16 and 17) made a study of the relative number of androgynous receptacles from several collections of *Dumortiera velutina* and *D. trichocephala*, showing that the former is chiefly dioecious and the latter monoecious. Later he reports in much detail

* Botanical Contribution from the Johns Hopkins University No. 121.

on the relative number of androgynous receptacles, and the relative proportion of male, female, and bisexual receptacles on the same thallus in these collections. He comes to the conclusion that the androgynous inflorescence here is a secondary or recent development: that is, dioecious species are primitive among the *Marchantiaceae*, monoecious forms are derived, and the androgynous receptacles are the culmination of this tendency. Heitz (31) puts the number of chromosomes for *D. hirsuta* at nine.

All of the *Dumortiera hirsuta* material used in this study was collected from the one station near Columbia mentioned above, except for one lot showing various stages of antheridial and archegonial development, which was collected in Jamaica, B. W. I., July 1932. *Dumortiera hirsuta* was found in two other localities about Columbia but all these plants have been sterile. Most of this material was fixed in either formol-acetic-alcohol, or in chrom-acetic osmic mixtures. The haematoxylin and various anilines, singly and in combination, were used for staining. The method that proved most efficient and convenient for general developmental stages was over-staining the sections in saffranin and reducing the saffranin to the desired point with Bismarck brown.

The development of *D. hirsuta* in Columbia is seasonal, whereas in Jamaica the various organs are initiated apparently any time of the year. A typical schedule of development for *D. hirsuta* at the Columbia station recorded in 1932-33 is as follows:

- August 11-19. All male receptacles were initiated.
- September 5-12. All female receptacles appeared.
- September 10-20. Spermatogenesis occurred in most antheridia.
- September 15-25. Most archegonia matured.
- September 25 to October 5. Majority of fertilizations occurred.
- October 5 to October 15. Young embryos have formed.
- October 15 to November 3. Foot and archesporium differentiated.
- November and December. Growth of sporophyte, formation of spore mother cells, and differentiation of elaters.
- December 20 to January 20. Growth of capsules and spore mother cells completed. Antheridial branches withered.
- January 26 to February 4. Meiosis occurred.
- February. Maturation of spores occurred, elaters, and cells of capsule wall thickened.
- March. Blackening of capsules, fertile thalli dying, and receptacles elongated.
- April. Setae elongating and spores liberated.

In dry years this schedule is somewhat modified.

THE FORMATION OF THE RECEPTACLES AND SEX ORGANS

The thallus of *Dumortiera hirsuta* grows by a wedge-shaped four sided apical cell located in a notch at the end of the branch. The notch is the result of the more rapid growth of the lateral tissue derived from the apical cell than of that immediately behind it. In a sagittal section also the apical cell occupies a notch and is nearer the ventral than the dorsal surface because the dorsal region grows more rapidly than the ventral and projects somewhat over the latter. Ventral scales are initiated on either side of the median sagittal plane. These scales overlap each other and the proximal ones project over the apex of the thallus as is common in the *Marchantiaceae* (Douin 12). The ventral scales often consist of a short limb with two wings, each covering a rhizoidal bundle. There is one main rhizoidal groove and several smaller lateral ones at first at the branch apex, though the ventral scales disappear early and both the plain and the peg rhizoids then lie free on the smooth ventral surface a few millimeters from the growing tip.

The Male Receptacle. The male receptacle commences as a slight mound of tissue pointing diagonally downward. The products of the apical cell, instead of maturing rapidly, remain actively meristematic and the apical cell becomes obscured. Soon a short downward pointing arm of rapidly growing tissue has been formed (fig. 106). The proximal half now commences to thicken up thus forming the primordium of the head, at the distal end of which are now distinguished several apical cells (fig. 107). Soon after the commencement of the male receptacle, all of the tissue at the base of the receptacle is morphologically ventral—witness the appearance of ventral scales on the upper side of the primordium in figure 106.

With the marking out of the apical cells, the proximal segments become the dorsal surface, the distal ones forming the ventral surface of the head. The stalk with its two ventral grooves is thus morphologically a ventral process. The size of the head is increased at first by divisions of all of the cells of the surface in addition to the tissue added by the apical cells. More rapid growth on the lower side of the stalk pushes the receptacle upward carrying it beyond the dorsal lip of the thallus. Sometimes growth is so much more rapid on the lower side that the head region is distinctly formed there before it has commenced to differentiate on the upper side. Antheridia always appear first on the lower side. The tissue at the top of the stalk just under the head remains slightly meristematic, gradually raising the maturing antheridial receptacles slightly above the thallus.

The Antheridium. When the male receptacle has attained a diameter of 0.6 to 0.8 millimeter, it commences to form antheridia. These are formed in radial series from the dorsal segments of each one of the apical cells. Antheridia are formed from about 20 to 25 apical cells each giving rise to a succession of 3 to 5 antheridia. As in the other marchantiaceous genera, the antheridia become sunken in pits on the lateral and dorsal surface accompanied by several (up to four) one to two celled glandular paraphyses. The terminal portions of these paraphyses are sometimes swollen. They persist only during the younger stages of the antheridia.

The antheridia become displaced as they mature so that in a section parallel to the dorsal surface of the receptacle the hundred or more antheridia are not in radiating rows but are considerably displaced, differing in this respect from *Marchantia* as Campbell (9) has pointed out in describing *D. velutina*. The antheridial initial is seen as a cell standing free from those surrounding it (fig. 1), recognizable within 2 or 3 cells of the growing point. It does not protrude above the general level of the thallus as in *Marchantia* (Strasburger 52). The initial now divides to a series of four cells in a row (figs. 2, 3, and 4), and is soon overgrown by the adjacent tissue of the thallus thus leaving the antheridium in a pit (figs. 2 and 3), as in *Marchantia* (Durand 14). Anticlinal walls appear and usually 2 to 4 central cells have divided when the antheridium is 6 cells long leaving only the stalk cell and terminal cells undivided. Figure 9 shows the cross-section of an initial consisting of a single row or cells; figure 10, the cross-section of a central cell of an antheridial initial showing the first longitudinal anticlinal division. Figure 11 shows that the next anticline is at right angles to the first dividing the central portion of the filament into four cells. Figure 5 shows an antheridium 8 cells long with the central 3 divided by anticlinal walls. Here the stalk and the body of the antheridium have already become differentiated. In figure 6 the anticlines have divided the cells at the tip of the antheridium whereas in figure 7 the anticlines have gone through the antheridial stalk, though this does not usually occur until considerably later. In figure 6 anticlines separating the inner spermatogenous tissue from the antheridial wall have commenced at the lower portion of the antheridium proper and are extending towards the cap cells. In figures 7 and 12 the spermatogenous cells are seen to have formed. Figure 8 shows that the spermatogenous tissue has commenced to divide further and figure 13 shows a cross-section at a slightly later stage. The antheridium is increasing in size all the while but does not

keep pace with the increase in spermatogenous cells, resulting thus in smaller cells as division continues. Figure 14 shows a nearly mature antheridium with its cap cells protruding into an apiculate tip as in *Riccia*, *Targonia*, or *Fimbriaria*. The stalk is two cells in section and is long and slender, differing from *Fimbriaria* and *Marchantia* in this respect, but similar to *Targonia* as figured by McFadden (39). When mature, an antheridium contains within wide limits, about fifty thousand antherozoids or about five million per male receptacle. This estimate for the antheridium is somewhat smaller than the figures given by Johnson (36) for the antheridium of *Monoclea*. The wall cells of the antheridia are turgid throughout development. The antheridia open by a terminal rupture, but no details here were observed.

The formation of a row of 3 or usually 4 cells in the antheridial filament agrees with Campbell (9) for *D. velutina*, Strasburger (52) for *Marchantia polymorpha*, Dupler (13) and Haupt (28) for *Reboulia hemisphaerica*, and McFadden (39) for *Targonia* though it may be 4 or 5 cells long before anticlines commence in *Monoclea* (Johnson 35) and *Fimbriaria* (Campbell 10). Anticlinal walls commence at the center of the antheridial filament, differing from *Reboulia* in this respect (Haupt 28). The periclinals to form the central cells begin in the lower portion of the antheridium, corresponding to *Marchantia* (Durant 14), and differing in this respect from *Reboulia* (Haupt 28). The separation of the central cells is typically marchantiaceous, the lowest row remaining sterile and forming the basal wall of the antheridium.

Spermatogenesis. The development of the spermatogenous tissue progresses unevenly in regard to cell division. Certain blocks of cells undergo mitosis simultaneously, though these regions do not necessarily coincide with an original spermatogenous cell or group of cells, although at times this appears to be true.

The last or diagonal division is probably the tenth or eleventh mitosis in the antheridium after the spermatogenous tissue has been differentiated. It commences earlier in some parts of the antheridium than in others though the developmental stages of the androcyte, to use Allen's (1) terminology, to form the antherozoids, are remarkably uniform throughout the antheridium. All of the antheridia of one receptacle produce antherozoids within a short time of each other, those at the periphery of the receptacle, being younger, maturing last.

The best preparations here were obtained with Haidenhain's iron haematoxylin stain after fixation with Flemming's strong solution. The formation of the androcyte is preceded by the diagonal division. This

division was followed in detail. Ten chromosomes were seen in the last division. No centrosomes here or in the earlier divisions of the spermatogenous tissue were seen. The other features of the last division here correspond closely to those observed in other *Bryophyta* [Ikeno (33); Wilson (56); Woodburn (57, 58, 59); Allen (1); Sharp (49); etc.].

The nucleolus now divides as though in preparation for another division. About this time, or sometime earlier, a granule appears in the cytoplasm some distance from the nucleus (figs. 49 and 50). It is larger and somewhat more diffuse than it later appears when it has moved to the proximity of the nucleus. This is the blepharoplast. The blepharoplast is identified with the centrosome in the case of *Marchantia* by Ikeno (33), of *Fegatella* by Bolleter (8), of *Pellia* by Wilson (56), of *Polytrichum* by Allen (2) and Walker (55), and of *Blasia* by Sharp (49). The blepharoplast is considered of possible centrosomic origin in *Plagiochila* (Johnson 36). It originates in the cytoplasm in *Riccia* according to Black (6), and Lewis (38) considers it a centrosome-like structure. Woodburn (57, 58, 59) considers the blepharoplast to be of cytoplasmic origin in all the forms he investigated: *Mnium*, *Asterella*, *Blasia*, *Porella*, *Marchantia*, and *Fegatella*. Wilson reports that the blepharoplast arises from a fragment of the nucleolus that passes to the cytoplasm in *Mnium hornum* and *Atrichum undulatum* and Bagchee (4) thinks it is of nuclear (chromatin) origin in *Anthoceros*.

From the work done on spermatogenesis among the bryophytes thus far, it seems safe to conclude that a centrosome-like body is often present in the last division of the spermatogenous tissue and the centrosome becomes transformed to a blepharoplast in the maturing androcyte. We might look upon cases where a blepharoplast still appears in the cytoplasm after the penultimate division, as an example of the retention by the plant for a special function in the spermatozoids of a body (the centrosome) which has ceased to exist in the vegetative cells.

The nucleolus sometimes cuts off two or three granules of varying sizes. These may evidently be formed in rapid succession, as they are sometimes seen to lie in a short chain. At this time the blepharoplast is already present in the cytoplasm. One of the larger nucleolar granules remains as the nucleolus of the maturing antherozoids, and soon shows an areola. The other fragments disappear from the nucleus eventually, but whether they degenerate or pass to the cytoplasm is uncertain. A "perenosome"-like body (Allen 2) is seen in the young androcyte. It is

a hyaline, spherical body with a granule at its center. This structure disappears in the maturing androcyte.

The story of the formation of the androcyte is that typical for bryophytes. The blepharoplast lies near the nucleus. It elongates at first to form a thick rod, but later becomes a long thin thread in intimate connection with the elongating nucleus and projects a considerable distance anteriorly (figs. 52-59). Figure 58 shows a nucleus so displaced that the extent of the blepharoplast can be seen. The nucleus after elongation has set in becomes somewhat flattened in a plane parallel to the diagonal wall mentioned, and then curved. By continued elongation and curving, the nucleus together with the blepharoplast soon gives the young antherozoid the appearance of a ring. It is really a watch-spring-like coil of about $1\frac{1}{4}$ turns. About this time the nucleus stains so deeply that it remains black with haematoxylin when destaining has gone far enough to make the other structures of the cell quite distinguishable. As the nucleus elongates further it becomes a cylindrical body tapering toward both ends. Preparations of such stages that have been destained until translucent show the nucleolus with the originally round areola much elongated. The nucleolus was not seen in mature antherozoids.

The formation of the two cilia was not seen. They can be observed after they have become rather long (fig. 59). Figures 60-64 were drawn from smears made from teased antheridia, and show stages in the rolling back of the cytoplasm to form the vesicle at the posterior end of the antherozoid. The cilia are long; one is attached at the anterior tip of the antherozoid, the other, somewhat posteriorly. Steil (51) found the cilia to be attached thus in *Riccardia*. The cilia are 3 to 4 times as long as the body of the antherozoid, the posterior cilium being longest. The following are usual dimensions: body of antherozoid 13 microns in length, anterior cilium 32-37 microns, and the posterior cilium 46-55 microns. Figure 64 shows the antherozoid dried and stained in a position characteristic of its active form.

By the time the sperm nucleus has elongated to form a ring the walls of the androcyte mother cells have become difficult to demonstrate. In the mature antheridium all cell walls of the spermatogenous tissue have disappeared. The androcytes lie closely packed in pairs in a mucilaginous medium. Campbell (9) reports the "sperm cells are not so evidently in pairs" in *D. velutina*. Upon ejection of the antheridial contents into water the cilia of the androcytes vibrate violently, freeing themselves from each other and from the mucilaginous matrix.

The Female Receptacle. Both male and female receptacles are borne on the same thallus, all the plants observed being monoecious. Female receptacles are initiated in a similar manner to the male receptacles. They become recognizable when the apical tissue of the head commences to form a narrow, ventral scale-free meristematic zone (fig. 108). Archegonia commence to be initiated when the receptacle is about 0.7 of a millimeter in diameter. These are formed in acropetal succession from each of the 7-15 growing points differentiated on each head. Campbell (9) reports 6-7 "apices" for *D. trichocephala*. There are usually three archegonia formed from each apical cell. These are formed in rapid succession in one radial row on each growing point as indicated in figure 15.

The Archegonium. The development of the archegonium is typically marchantiaceous, and follows the development given by Campbell (9) for *D. trichocephala* closely. A surface cell of the lower side of the receptacle divides to form a stalk and an archegonium initial (figs. 16 and 17). This initial protrudes beyond the level of the thallus and often is somewhat larger than the stalk, as was shown by Strasburger (52) for *Marchantia*. The stalk cell may be divided by a partial or usually complete longitudinal wall before the archegonium initial has divided (fig. 17). The archegonium initial is divided by the usual three longitudinal walls (figs. 15, 18, and 26). A transverse wall then appears separating the cap cell from the central cell (fig. 21). The central cell then divides in the usual way to form the egg cell, the ventral canal cell, and the neck canal cells (figs. 15, 20, 27 and 28). Figure 25 shows a transverse section through an archegonium at such a stage as figure 22 after a division has occurred in a wall cell. The ventral canal cell disintegrates long before the neck canal cells, forming a dark mucilaginous cap on top of the egg. Although mitotic figures were seen only in the divisions of the neck and the neck canal cells, the origin of the various cells of the archegonium can be identified rather certainly by the slight difference in cell size, cell wall placement, and density of cell contents. The neck of the archegonium at maturity is usually 6 cells in circumference (fig. 23) occasionally 7 (fig. 24). Six is the typical number for the *Marchantiaceae* (Janczewski 34). Johnson (35) found that the necks of the archegonia in *Monoclea* show 5-8 cells in cross section. The neck of the archegonium elongates as maturity is reached until it is 20-25 cells long, those nearer the venter being short and increasing in length as the apex is approached. The mature archegonium is somewhat larger than that reported for *D. trichocephala* by Campbell (9).

and is longer than in *Marchantia* (Durand 14) though not as long as that of *Fegatella* (Janczewski 34). At maturity the neck bends outward and upward around the edge of the receptacle. Thus the tips of the archegonia lie in the angle just below the upper surface of the head and next to the outwardly protruding ventral scales. An unopened tip in optical section is shown in figure 30 and an opened unfertilized archegonium in fig. 31. A surface view of an opened fresh archegonium is given in figure 32, showing 5 turgid cap cells which have slightly thickened outer walls and are separated somewhat from each other and from the neck cells. Soon after opening, the neck canal cells degenerate completely. The egg lies surrounded by the mucilaginous remains of the ventral canal cell. During the development of the archegonium the wall of the venter has become 2 and 3 cells in thickness in which it differs from *Marchantia*, *Preissia*, and *Lunularia*, but resembles *Plagiochasma* and *Reboulia* (Janczewski 34), and *Monoclea* (Johnson 35). The ripe egg normally fills the venter. The nucleus and its nucleolus are large. There is no receptive spot.

Occasionally abnormal archegonia are seen. One such abnormality is figured (fig. 29) showing the egg, ventral canal cell, and neck canal cells in duplicate. Another abnormal archegonium lacked a venter, a neck canal cell becoming apparently the egg cell. Still another variation was observed where a single egg and ventral canal cell were followed by a double series of neck canal cells.

The Involucre. Usually after the formation of the third archegonium from any one growing point of a receptacle the apical cell becomes inactive as such and is carried up by a ring of tissue (all of the marginal cells of which are two sided in radial section) surrounding the archegonial group on the axial and lateral sides. This is the commencement of the involucre. Occasionally two involucre are initiated, the inner one growing up about a single archegonium. There is no perianth developed. The distal side of the archegonial group is usually bordered at first by the overhanging edge of the receptacle. The involucre is not the result of fertilization and in this respect is similar to that of *Monoclea* (Johnson 35). At the time of fertilization the involucre is about the same height as the venter of an archegonium. With further growth of the involucre its abaxial portion differentiates from the ventral tissue of the edge of the receptacle. Growth of the whole female receptacle now takes place on all radii where fertilization has occurred. The opening of the involucre narrows and by the time sporogenous cells in the embryo have become elongated and separated from each other,

the involucre has become a closed pointed sac surrounding the enlarging venter of the archegonium and closed about the neck end of the latter. This involucre differs from that of *Conocephalum* as described by Graham (25) where more rapid growth on the axial side of the involucre (in the latter) brings the point of closure nearly opposite the foot of the sporogonium. The growth of the involucre is more rapid than the enlarging embryo, thus leaving a considerable space between the two. The mature involucre bears numerous bristly hairs.

Bisexual Receptacles. Bisexual receptacles were first reported in the *Marchantiaceae* in *Dumortiera irrigua* by Taylor (54). Such receptacles have since been observed in various other *Marchantiaceae* as has been noted in a review by Haupt (30). A detailed study of these bisexual receptacles in *D. trichocephala* and *D. velutina* was made by Ernst (16, 17). He found them common in the former species but rare in the latter. Bisexual receptacles were found frequently in the Jamaica collection where about half of such receptacles were typically male, the other half female. However, bisexual receptacles vary from predominantly male to predominantly female, the various radii being either wholly male or female. There is no alternation of radii of different sexes, those of the same sex always adjoining each other. Bisexual receptacles occur rarely at Columbia, only two being found out of the hundreds of receptacles observed.

THE DEVELOPMENT OF THE SPOROPHYTE

Fertilization. No observations were made in the living plant on fertilization. After the entrance of the sperm, the male nucleus enlarges considerably becoming elongated at first. This agrees with the structure of the male nucleus of *Sphaerocarpus* according to Rickett (47). In *Riccardia*, the sperm nucleus becomes longer and more attenuate during and after penetration of the egg as shown by Showalter (50). The nucleolus of the male soon becomes visible and the nucleus rounds up. Both the male nucleus and its nucleolus are considerably smaller than the corresponding ones of the female. A membrane soon surrounds the egg (fig. 36). Judging from the frequency of the appearance of two separate nuclei in the egg, it is assumed that there is a considerable period after the entrance of the antherozoid before the fusion of the two nuclei takes place. The male nucleus approaches the female nucleus (figs. 35 and 36), and gradually merges with it (fig. 37). Here a distinction between the chromatin net of the egg and that of the sperm can yet be seen. At a slightly later period the two reticuli are

indistinguishable and the nucleoli are in the process of fusing (fig. 38). The chromatin was not seen to emerge from the reticulate phase as described in *Corsinia* and *Fegatella* by Meyer (41, 42), in *Sphaerocarpus* by Rickett (47), in *Riccia* by Black (6) and Garber (23), in *Preissia* by Graham (26), and in *Riccardia* by Showalter (50). The fertilized egg remains undivided for a considerable period, during which the venter of the archegonium enlarges and becomes four or five layers thick (fig. 33).

The Embryo. Fertilization may take place in all of the archegonia of any involucrel group and embryonic development begin. One embryo, however, soon takes the lead, the suppressed embryos rarely developing beyond 2-8 cells. The fertilized egg elongates before the first division, the mitotic spindle lies in its axis and the cell divides to two usually approximately equal halves by a wall transverse to the longitudinal axis of the venter (fig. 39). Occasionally the epibasal cell may be larger as in *D. velutina* (Campbell 9) and the first wall may often also be somewhat oblique. The next wall may be transverse also, forming thus an embryo of three cells in a row as reported for *D. velutina* (fig. 42). In other cases the next walls may be perpendicular to the first, dividing the embryo into quadrants (fig. 40). In the quadrants the next walls are vertical thus dividing the embryo into octants (fig. 41). In the filamentous embryo (fig. 42) are shown vertical walls after several have appeared, whereas in the 8-celled embryo shown in fig. 43, the vertical walls have appeared in a plane parallel to the section, and the distal region has commenced to subdivide. The octant type of embryo found here occurs also in *Marchantia polymorpha* (Durand 14), *M. domingensis* (Anderson 3) *Riccia* and *Targonia* (Campbell 10), *Preissia* (Haupt 30), *Riccio-carpus* (Garber 23), though in the latter it may sometimes form a row of cells, and *Oxymitra* (Sealey 48). Meyer (41) considers the quadrant type to be more advanced than the "filamentous" one. Admitting this then, *Dumortiera* may be considered intermediate in this respect between *Marchantia* on the one hand and *Conocephalum* or *Reboulia* on the other. Anticlinal and periclinal walls now come in irregularly forming a sphere of tissue (figs. 44-48), as in *Marchantia* or *Oxymitra* (Sealey 48). The capsule wall and primary archesporial cells are delimited by longitudinal periclinal walls (fig. 44). The venter of the archegonium increases considerably in size during the early development of the embryo. Its wall becomes 8-10 cells in thickness by the time the sporogenous tissue begins to stain differentially—and thus differs in this respect from *Marchantia* (Durand 14). Further enlargement of the venter or calyptra to accommodate the growing sporogonium is not accompanied by

further growth in thickness of its wall. The original quadrant walls are indicated diagrammatically in figures 45 and 47. Figure 48 shows a longitudinal section of an embryo in which the sporogenous tissue is being differentiated. It is possible that the capsular region of the embryo is formed from the epibasal cell of the embryo, and the foot and stalk regions, which never become markedly differentiated, are produced by the hypobasal cell. The sporogenous tissue stains more deeply and becomes distinguishable from the wall cells of the capsule while the embryo is still spherical (fig. 48); the basal portion of the embryo embedded in the floor of the venter becomes the haustorial zone. The sporogenous cells continue to grow and to divide, chiefly by longitudinal walls. Thus as the embryo enlarges the sporogenous cells become elongated in the direction of the axis of the capsule (figs. 109 and 110). No cap or extra layer of sterile cells remains at the apex of the capsule as in *D. trichocephala* (Campbell 9), *Marchantia chenopoda* (McNaught 40), *M. domingnensis* (Anderson 3), or *Fegatella* (Meyer 42).

The cells within the capsule continue to elongate and later separate from each other. The young elaters and definitive sporogenous cells are not as yet different in appearance. The cells at the center of the capsule are always longer and narrower than those near the periphery (figs. 65-68). These sporogenous cells are longer than in *Marchantia*. The nucleus now elongates in the sporogenous cells, and divides (figs. 70-73). Cross-walls were not demonstrated at this stage (fig. 74). Later, the cytoplasm increases about each nucleus giving the hitherto spindle-shaped cell a nodular appearance (fig. 75). After the third nuclear division, cross walls become clear and thus a chain of 8 (or perhaps more) spore mother cells is finally formed (figs. 82 and 111). The cells destined to form elaters, on the contrary, continue to elongate greatly (fig. 69), but their nuclei never divide. Though the spore mother cells hang together in chains at first they are readily separable before divisions in these cells are completed. As divisions of the nucleus of the sporogenous cell take place, spore mother cells are formed in the middle region of the original cell. This leaves the two more or less attenuate ends of each sporogenous cell attached to the terminal spore mother cell of each series (figs. 80 and 82). The row of spore mother cells shown in figure 82 was formed from a sporogenous cell such as is shown in figure 65, while the terminal spore mother cell such as that shown in figure 80 was formed from a cell as shown in figure 68. The process referred to is finally digested and the terminal spore mother cell rounds up to resemble the other spore mother cells of the chain. A single layer of

sporogenous tissue next to the capsule wall does not develop into spores and elaters but disintegrates, forming a sort of tapetal addition to the mucilaginous content of the capsule, an apparently unusual condition in the liverworts. The spore mother cells later separate and round up though they still lie in rows (fig. 111). When first formed they measure 11 to 13 microns in diameter and their nuclei are about 7.6 microns (figs. 76 and 77). The spore mother cells continue to increase in size (figs. 78 and 79) and the elaters continue to elongate. The mature mother cells are approximately twice their original size (26–27 microns in diameter, with nuclei 13 microns in diameter) (fig. 81); while the elaters have attained a length of about 700 microns.

This increase in size is at the expense of the dense cytoplasm of the young spore mother cell, the mature spore mother cell being rather vacuolate here as it is in *Corsinia* (Meyer 41). The ripe spore mother cell is spherical, as is typical of the *Marchantiaceae*. Dense mucilage fills the interstices between the spore mother cells and elaters. This becomes thinner and finally disappears during the maturation of the spores.

Meiosis. Various fixatives were tried for this stage of development, those proving most efficient were Flemming's strong, and the Chicago modification of Flemming's as listed by Chamberlain (11). The sporangial wall at the time of meiosis is an effective barrier to the penetration of fixatives of the chromic acid series, consequently, to facilitate fixation, one-fourth to one-third the diameter of each sporogonium was cut away. Contrary to what might be expected few spore mother cells were lost. Even when the spore mother cells were thus exposed, the fixation was often incomplete and some plasmolysis was evident in the center of the sporogenous mass. The stains most effective after fixation were either saffranin alone or in combination with gentian violet or Bismarck brown, or Flemming's triple stain. Varying schedules for Heidenhain's haematoxylin were tried but, as Blair (7) also found true in the case of *Reboulia*, good differentiation was not obtained. Sections were cut from 3–5 microns in thickness.

There was no observed periodicity in the mitoses. Lots were fixed at various hours of the day and night but metaphases appeared in about the same proportion (about 10%) no matter when the sporogonia were fixed.

No evidence could be found in the fixed material of amoeboid movement of the spore mother cells noted for instance by Haupt (29) in *Reboulia* and Moore (44a) in *Pallavicinia*. The spore mother cells of

Dumortiera are round and their nuclei are round and turgid unless shrunken by poor fixation. No accurate data were obtained regarding the time involved in the reduction division. It must be very short since on January 30, 1933, few tetrads were formed, and by February 4, very few prophase were encountered. After prophase is well advanced the process must be very rapid since there exists no resting period between the two divisions and figures of both divisions are sometimes seen in the same capsule.

During the ripening of the spore mother cell, kinoplasmic plates make their appearance (fig. 81). They were seen only in the meiotic phase of *Dumortiera*. They seem to be characteristic of this phase in a number of forms: noted in *Pallavicinia* by Moore (44a), *Fegatella* by Meyer (42), and in *Reboulia* by Blair (7). In *Dumortiera* Gram's stain revealed elliptical bodies in these plates (fig. 91). They were never seen in material stained with safranin alone or in combination. The ripe spore mother cell is surrounded by a wall about 0.5 micron in thickness. The prophase, judging from the frequency of its appearance (about 50% of the capsules), occupies a considerable time. The first indication of its commencement is the enlargement of the nucleus and the rearrangement of the linin to form a spireme. This spireme is poor in staining substances as was noted by Farmer in *Fossombronia*. Spiremes have been seen by various workers in this field: Moore found a definite double spireme in *Pallavicinia* which after contraction broke up to form chromosomes; Meyer (41) found a synaptic spireme in *Corsinia*; Florin (22) found the same condition in *Chiloscyphus*; Beer (5) found a spireme in *Riccia*, Meyer (42) in *Fegatella*, and Graham (26) in *Preissia*. In *Dumortiera* the spireme appears as an extremely fine, highly convoluted thread, apparently continuous (fig. 83).

The spireme then undergoes synapsis, contracting toward one side of the nucleus (fig. 84). The nucleolus is usually located at one edge of the knot, and partially embedded in it. The release of the spireme from synezeis soon takes place, and it again fills the whole nucleus (fig. 85). The chromatin granules are becoming more conspicuous. The spireme begins to contract to the periphery of the nucleus against its wall (figs. 86 and 87) as was noted in *Fossombronia* by Farmer (21). Here the chromatin granules become fewer and larger and most are grouped in pairs. With the retreat of the spireme to the nuclear wall, a continuous spireme seems to give way to irregular wefts on which are disposed chromatin granules. Blair (7) noted a similar character in the post-synaptic spireme. The paired chromatin granules give the only evi-

dence of a possibly double spireme. These chromomeres seem to fuse until paired chromosomes are found at the periphery of the nucleus. Occasionally one or two of the pairs of chromosomes are formed in advance of the others.

Farmer (21) noticed that the chromatin granules in *Fossombronina* become aggregated along special thickened areas of a thread, and there condense to form chromosomes. Van Hook (60) reports that the linin is dissolved, the chromosomes then appearing; while Meyer (41) reports that the chromatin bodies of the nucleus of *Corsinia* fused to form chromosomes.

The nucleolus which has been visible throughout this process now rapidly disappears or at least loses its staining power and cannot be seen by the time the chromosomes are formed. The nucleolus may divide in two before the chromosomes have been formed, though it usually disappears before dividing. The nucleolus here, as well as in other phases of the plant, consists of a hyaline center surrounded by a deeply staining outer region giving it in optical section the appearance of a ring. No connection between any nuclear material and the nucleolus was observed. The nucleolus shows no signs of a fragmentation such as was noted by Farmer (21) and Blair (7) nor of a loss of chromatin or other substances. It seems to disappear rapidly, as faintly staining nucleoli are rarely seen.

The nuclear wall now disappears and a spindle is formed. The origin of the spindle is not clear though it seems to be formed within the nucleus, with the spindle fibers first appearing at the poles and later becoming visible across the equatorial zone. The axis of the spindle is perpendicular to the kinoplasmic plates and its poles push into the plates but have no organic connection with them. Moore (44a) says that the spindle originates from these polar caps in *Pallavicinia*. The origin according to Blair (7) is doubtful in *Reboulia* but the completed spindle projects into the cytoplasm. In *Dumortiera* these kinoplasmic plates have started to split in two when the spindle is formed and by anaphase of the heterotypic division these halves have often become separated. The poles of the spindle then lie between the separating half plates. Bivalent chromosomes arrange themselves on the equator of these spindles. There seem to be ten such pairs. Sometimes these dyads display a tetrad character as noted in *Fossombronina* by Farmer (21) and *Chiloscyphus* by Florin (22). That this did not appear to be a constant feature in *Dumortiera* is probably the result of the difficulty of accurate stain differentiation for such small chromosomes. The

heterotypic chromosomes in material fixed with the Chamberlain's modification of Flemming's fluid were strikingly larger (figs. 89 and 90) than the univalent chromosomes of the next or homeotypic division though the chromosomes of both divisions appeared of the same size in Flemming fixed material.

During metaphase the chromosomes of the dyads pull apart. They seem to be extremely viscous, threading out along the line of separation to such an extent that in some cases the bodies of the chromosomes were indistinguishable from the zone of separation, the two separating chromosomes appearing as an elongated thread thinning in the middle (fig. 92). The chromatin later pulls apart and condenses into typical chromosomes by the time anaphase is well advanced (fig. 93).

Figure 93 shows ten chromosomes in the lower group and nine in the upper. The tenth is not drawn in the latter but can be seen in the slide to lie under the chromosomal group. A pair of small chromosomes is here seen to lie in advance of the rest. These were often seen here. At times they had nearly reached the poles before the other chromosomes had fully separated. A count of ten can rarely be had in a polar view of a metaphasic plate on this account. This behavior of this small chromosome was not seen at any other cell division in the plant.

The manner of separation of the dyads is undetermined. The chromosomes become compacted together at telophase (fig. 96), the chromatin merging together but soon separating into a number of granules distributed on irregular wefts of linin. No spireme was seen to form in preparation for the homeotypic division. The nucleus of figure 94 corresponds to the phase seen in figure 87 except that the chromomeres are not in pairs in figure 94. Each nucleus is now about half the size of the previous prophase nucleus. The spindle fibers now become more numerous and a clear-cut cell plate is formed across them (fig. 94). When this plate has gone half way across the cell, the spindle fibers become distorted and give place to a thready vacuolate cytoplasmic meshwork. No distinct phragmoplast can be seen, though under favorable conditions the cell plate, which has now become a thickened, reticulate cytoplasmic band, is seen extended across the protoplast (fig. 97). The nucleolus reappears and is often seen to have divided into two. These daughter nuclei now become extremely elongated in a plane parallel to the previous cell plate, with the separated kinoplasmic plates lying at their poles (fig. 97). The nucleoli now disappear, the homeotypic spindles appear and the chromatin granules condense to form chromosomes and arrange themselves on the equator of the

spindle. Thus there is no true resting stage between the two divisions. The homeotypic spindles are somewhat more slender than the heterotypic ones (fig. 98). They may be parallel or at right angles to each other. Meyer (42) pointed out that these spindles were always parallel in *Fegatella* and Moore (44a) reports them as being perpendicular in *Pallavicinia*.

The separation of the split haploid chromosomes is rapid, the chromosomes reaching the poles and quickly becoming disposed as granules upon the reticulum. The outline of the nucleus remains irregular for a considerable time due to the adajutting cytoplasmic vacuoles (fig. 99). The spindle fibers rapidly disappear with the formation of a cell plate and four spores are formed in the manner described above. The peripheries of these four protoplasts soon take on definite margins, and become separated from each other by narrow spaces. Each of these four protoplasts now commences to secrete a wall about itself while the original wall of the spore mother cell has begun to dissolve. The nuclei of the spores now acquire a typical appearance, though they are often somewhat irregular in shape. They are delimited by a well-defined nuclear wall and contain a granular reticulum and a deeply staining nucleolus. The kinoplasmic plates disappear and the cytoplasm becomes somewhat thinner as the spore walls are formed.

MATURATION OF SPORES, ELATERS AND CAPSULE

Immediately after the formation of the spore tetrads, each spore protoplast separates somewhat from its neighbors and is delimited by its own plasma membrane (fig. 99). This membrane is seen in the ripening spore as a dark line on the interior of the other walls, slightly thickened in various regions due to cytoplasmic connections with the body of the spore. The protoplast now secretes an exospore, which soon reaches a thickness of 0.5–0.6 microns (fig. 100). A brown episore is then deposited upon the exospore. As a membrane the episore is thin, and it is continuous over the local thickenings or papillae of the exospore (fig. 101). These papillae attain a length of 1.6–1.8 microns. On the side next to a sister spore the ends are often bent due to the presence of the adjoining spore. The ends of these blunt spines are typically notched, but may be irregular or simple. With the development of the episore, the old spore mother cell wall is completely dissolved. The reserve food in the spores is of a soluble nature, the body of the spores in section being empty except for the nucleus, which is usually crowded to one side, and a few cytoplasmic strands branching through the body

of the spore. The nucleus is of medium size, having, when spherical, a diameter of about 5 microns. The spores hang together in tetrads for a long time (fig. 114). The ripe spore is about 30 microns long and 23 microns thick.

Normally spores are formed in tetrads, infrequently in diads, and rarely in triads.

By the time the exospore commences to form, a hyaline double spiral band 2.7–3 microns wide is being laid down on the inside of the wall of the elater by a band of granular cytoplasm following a similar course. It is in this same manner that the thickenings are formed in the elaters of *Fimbriaria* according to Campbell (10). The spiral band soon becomes thick and brown in color. They are closely wound in the middle region of the elaters, but become lax towards the ends (fig. 114). They are usually united at the pointed ends of the elaters. The mature elaters contain no cytoplasm. The elaters are 7.2 microns wide and 0.6–0.7 millimeter in length. The formation of spore coats and elater thickenings reduces the mucilaginous contents of the capsule to a minimum.

In the wall cells of the capsule at about the time the elaters commence to thicken, short spiral, annular, or incomplete annular thickenings are deposited by special bands of granular cytoplasm (fig. 112). The capsular wall is one cell in thickness. The mature capsule not only has thickened wall cells but also has a layer one to two cells thick at the base of the capsule thickened by annulations or short spirals. Many of these cells are conical in shape, 50 microns wide at their bases and their pointed ends protruding 100–120 microns into the capsule. These are best seen in hand sections of the fresh capsule after washing away the spores and elaters. These cells evidently represent transition stages between tissue of the seta and the elaters.

During the maturing of the sporophyte, the stalk of the female receptacle elongates. The growth here is slow. By the time the capsules are blackening the stalks are about 3–10 millimeters long; when the spores are shed, the stalks range from two to three centimeters in length. Receptacles of some of the plants of *D. hirsuta* observed in Jamaica had stalks measuring up to six centimeters.

Stalks of elongating female receptacles were marked at millimeter intervals while still comparatively short, with carmine which had been ground into vaseline. Further elongation of the stalk did not separate these markings, but took place above the markings at the base of the head of the receptacle. Sections reveal a meristematic zone at the tip of the stalk, ventral to the tissue of the head.

When the capsule has matured, the seta elongates and pushes the capsule through the calyptra and involucre, rupturing these tissue layers. This elongation occupies from one to two days. The capsule appears black while the seta is whitish, though a few small, green chromatophores are present. The sporogonia protrude in a diagonally downward direction.

Just before elongation takes place, the stalk of the sporogonium is about 0.6 millimeter in length, whereas afterwards the stalk measures 1.8–2.2 millimeters, that is three or more times as long as before. The number of cells in the seta is the same before and after elongation, there being about 15 cells in the length of the seta. Before the elongation of the seta its cells are cubical or somewhat elongate and measure 30–60 microns; after elongation these cells become three or more times as long as before, measuring 100–180 microns. Thus the total elongation of the stalk is effected by the lengthening of the cells composing it. In this it agrees with the seta of *Monoclea* described by Johnson (35).

The wall of the capsule is composed of rows of cells radiating upward from the seta which give way to cells irregularly placed in the apical region. The wall cells are thickened chiefly by annulations. As the cells of the capsule wall dry and the water leaves the cell cavities, atmospheric pressure evidently flattens the cell wall about the annulations. At the apex of the capsule, where the cells are irregularly disposed, the resultant contraction of the cells causes them to pull apart in irregular groups. Most of these groups of cells are flicked off by the elaters that now commence to writhe as they dry. A few of the fragments remain attached to the side wall of the capsule. There is no annulus, and there is no lid or cap that comes off. The drying of the sporogonial wall which causes the contraction of the cells now produces tears in the capsular wall which follow the lines of least resistance, that is, they run between rows of cells down the sides of the capsule. There is no predictable line of weakness, the split may follow a straight line between two rows of cells, or it may pass from one row to another, or it may be rather irregular in its course. The drying and expanding mass of elaters now assist in splitting the capsular wall. There are usually five to eight fissures initiated, three to five of these may run at least three quarters of the way to the stalk. When the capsular wall is dry it forms a small shrivelled crown at the upper end of the seta and the spores and elaters are exposed as a spreading tuft. Many of the spores are flicked off during this initial phase by the elaters, some of them being sent to a distance of three millimeters. The spores are gradually

dislodged by hygroscopic activity of the elaters, wind and rain, and distributed by air and water currents.

Many of the elaters as they elongate in the developing capsule force their pointed ends between cells at the base of the capsule for a short distance. Presumably these elaters prevent the everted tuft of spores and elaters from falling away readily *en masse* from the sporogonium.

In dry air, the capsules open by the time they have become completely exerted from the involucre, often commencing to open before this. In a saturated atmosphere in a covered dish they do not open, but they open promptly when placed in less humid air.

O'Hanlon (45) estimates the number of spores for *Marchantia polymorpha* at not less than 300,000 per capsule. In *D. hirsuta*, counts of samples of well agitated dilutions from single capsules give much smaller figures: 30-40,000 spores for small capsules and 75-85,000 for large ones.

GERMINATION OF SPORES AND THE FORMATION OF THE JUVENILE THALLUS

Spores were removed from capsules after they had become brown, or at the time of the extrusion of the capsule through the involucre. The spores were placed on pieces of unglazed clay pottery in 0.1 per cent Knop's solution in petri dishes. The pottery had been superficially cleansed and then boiled in several changes of distilled water to remove any soluble matter. The water of condensation on the petri dish covers was periodically wiped off, and this loss regularly replenished with distilled water. Every two weeks the Knop's solution was discarded and fresh 0.1 per cent added. The cultures were kept out of direct sunlight, but exposed to bright diffuse skylight. No noticeable contamination of the cultures occurred except for several types of small *Diatoms* whose numbers never became great. A spore before it commences to germinate is shown in figure 102 a.

After a week to ten days the spores commence to swell thus becoming spherical. They are now more transparent and have become greenish. The swelling is a growth process and not a mere mechanical imbibition of water. In two weeks, a rhizoid is seen to break through the spore coat and elongate (fig. 102 b and e). Sometimes the formation of the first rhizoid is delayed until after a two or three celled sporeling has been formed (fig. 103 a, b, and e). With the increase in size of the spore, the spore coat, which at first may have been ruptured at one or more points, is now progressively digested; so that by the time the primary cell has divided, or even before (fig. 102 f), all that remains of the spore coat is the undigested papillae now irregularly scattered on the surface

of the sporeling, since the latter has increased considerably in volume (fig. 103). Sometimes most of the papillae are left grouped in one to several patches on the posterior cell or cells.

All spores germinate but spores sown together under identical conditions, did not all germinate at the same time nor develop with the same rapidity. This difference became more pronounced as the cultures became older. After a month, the more advanced thalli had formed a marginal growing region as in figure 105 while those most retarded were 4-6 celled thalli.

After $2\frac{1}{2}$ weeks, the sporelings developing most rapidly had formed thalli of 2-5 cells (fig. 103). The numerous ellipsoidal chloroplasts are not drawn, but the exosporal papillae are indicated to show their scattering over the surface of the cells, and also to indicate the absence of a discarded spore coat. O'Hanlon's (45) figures for *Marchantia polymorpha* show no spore coat remaining on the sporeling, but she makes no remark upon the manner of its disposal. In *Fimbriaria* and *Targonia* however according to Campbell (10) and in *Reilla* according to Studhalter (53) and in others, the ruptured spore coats are left behind on the posterior cell of the sporeling.

The first division in the spore may or may not occur subsequent to an elongation of the spore cell. Rarely this elongation is pronounced enough to be considered as a "germ tube." The first divisions are very irregular. They usually follow one of two general lines of development. A filament of 3-5 cells may be formed, the anterior cell then dividing by a perpendicular anticleine to initiate the broad thallus which is now developed in one plane by periclinal and perpendicular anticleines. In the second type of development the filamentous stage is eliminated altogether. The two celled stage is spherical and one or both of these cells may divide by walls perpendicular to the first, thus forming respectively two or four quadrants. Octants may now be formed, though usually one or more quadrant cells fail to divide thus resulting in a wide variation of forms. One to several of these octants or quadrants divide to form the broad thallus, the other cells rapidly mature. The posterior cell gives rise to a rhizoid, if this has not already occurred. Figures 104 a, b, and c show young thalli initiated from the filamentous type of germination. The original line of cell division here is rendered vague because the cells are distorted by turgor. Figures 104 d, e, and f show that the spore has developed directly into a thallus. Spores were germinated in two rooms: those exposed to longer periods of bright

skylight followed the latter mode of development, those exposed to shorter periods followed the former.

Occasionally longitudinal anticlines rendered the thallus two cells in thickness locally, though the thallus is often apparently or incompletely so due to the crowding and overlapping of these large turgid cells.

Figure 105 shows young thalli after further development of the anterior cells as they initiate a marginal growing region. The cells are becoming progressively smaller, but this decrease in size is overcompensated by the increase in number of cells, thus a progressively widening thallus is developing. Such a smooth growing margin as in figure 105 d and e is established in 5-6 weeks after sowing the spores. Two margins may be formed instead of one, thus resulting in branching. A transient apical cell is sometimes established early (fig. 104 g) but never persists, being soon replaced by the series of marginal growing cells in which no distinctly leading individual cell is discernible.

The thalli develop more rapidly where no actual film of water covers the plants. This was prevented by sowing spores over a cleansed, inverted flower pot kept in a covered glass jar at the bottom of which was half an inch of 0.1 per cent Knop's solution. The spores grow more rapidly at the top (base) of the pot where it was merely damp. No effort was made to control room temperature.

Thalli all grew in one direction in undisturbed cultures, indicating that light is the controlling factor in polarizing the young thallus: they grow perpendicular to the direction of incident light. Spores do not germinate in the dark.

With the formation of a meristematic margin, growth proceeds by each cell of this marginal row dividing by a wall parallel to the margin. The proximal series now divide by horizontal anticlines thus rendering the thallus two cells in thickness. These cells now mature. Most of the distal cells divide by vertical and longitudinal anticlines, thus producing nearly twice the number of marginal cells. Thus an individual row of cells near the margin as one passes from the posterior anteriorly appears to be incompletely dichotomous, though this effect is soon lost. Failure of one or more adjoining marginal cells to divide further initiates two branches. Rhizoids appear on the posterior ventral surface. They are thin-walled and smooth.

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SUMMARY

1. *Dumortiera hirsuta* at Columbia, S. C., commences to form antheridia the last of August and liberates its spores the first of April. No strict seasonal development was observed in Jamaica, B. W. I.

2. The male or female receptacle originates as a multicellular meristematic process, the development of which is typical.

3. The development of antheridium and archegonium was traced, and this is found to be typically marchantiaceous.

4. No centrosome was seen in any mitotic divisions. The blepharoplast of the androcyte arises apparently independently in the cytoplasm. The elongation of the blepharoplast and elongation of the nucleus of the androcyte, and the formation of the mature sperm are typical for the *Hepaticae*.

5. Approach of the sperm nucleus to the egg nucleus and the fusion of these were observed. The fertilized egg underwent a brief period of rest before the formation of the sporogonium commenced.

6. The first two divisions of the embryo may form quadrants or a filament of three cells.

7. The development of the sporogenous tissue was traced and meiosis in the spore mother cells was observed. The first division in the latter was heterotypic, there being ten diads.

8. The maturation of the spores, elaters, and capsule is typically marchantiaceous.

9. The female receptacle elongates from 2-6 centimeters by an intercalary meristematic zone at the upper end of the stalk of the receptacle.

10. The seta of the sporogonium elongates solely by growth in length of these cells and not by cell division.

11. The capsule of the sporogonium opens into several irregularly split flaps.

12. The spores germinate in ten days in Knop's solution in strong diffuse light.

13. The germinating spore digests the exospore except for its papillae.

14. A flat juvenile thallus is formed that grows perpendicular to the direction of incident light by a marginal growing zone.

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EXPLANATION OF PLATES

PLATE 4

- Figs. 1, 2, 3, and 4. Longitudinal sections of young antheridia before first longitudinal anticlinal walls are formed. $\times 325$.
- Fig. 5. Longitudinal section of antheridium showing first longitudinal anticlinal walls. $\times 325$.
- Fig. 6. Longitudinal section showing spermatogenous cells being cut out. $\times 325$.
- Fig. 7. Similar section showing spermatogenous tissue completely cut out. $\times 325$.
- Fig. 8. Longitudinal section of slightly later stage showing submergence of antheridium by more rapid growth of surrounding tissue. $\times 325$.
- Figs. 9, 10, 11, 12, and 13. Series of transverse sections through bodies of five antheridia showing steps in development. In figure 12 spermatogenous tissue is delimited. $\times 325$.
- Fig. 14. Median optical longitudinal section of a nearly mature living antheridium $\times 85$.
- Fig. 15. Longitudinal section of two young archegonia; involucre commencing to form at right. $\times 325$.
- Fig. 16. One apical cell of a female receptacle showing a two-celled archegonial rudiment at left. $\times 325$.
- Fig. 17. Similar section showing stalk of archegonial initial divided. $\times 325$.
- Fig. 18. Similar section with more advanced archegonium. $\times 325$.
- Figs. 19, 20, 21, 22. Longitudinal sections of further developmental stages of the archegonium. $\times 325$.
- Fig. 23. Cross-section of the neck of a mature archegonium. $\times 325$.
- Fig. 24. Same, before neck canal cells had disintegrated. $\times 325$.
- Fig. 25. Cross-section of the body of the archegonium of such a stage as figs. 21 or 22. One of the three original wall cells has divided. $\times 325$.
- Fig. 26. An archegonium as in figure 18 showing the three vertical walls in section. $\times 325$.

Figs. 27 and 28. Longitudinal sections of later developmental stages of the archegonium. $\times 325$.

Fig. 29. Longitudinal section of basal part of an abnormal archegonium with two eggs, two ventral canal cells, and a double series of neck canal cells. $\times 325$.

Fig. 30. Optical section of the tip of a living unopened archegonium. $\times 325$.

PLATE 5.

Fig. 31. Longitudinal section of a mature, opened, unfertilized archegonium. $\times 325$.

Fig. 32. Surface of tip of an opened archegonium. $\times 325$.

Fig. 33. Cross-section of the venter of an archegonium containing a fertilized egg. $\times 325$.

Fig. 34. Longitudinal section of venter showing egg and sperm soon after entrance. $\times 325$.

Figs. 35, 36, 37, and 38. Parts of similar sections showing approach of male nucleus and three stages of fusion with egg nucleus. $\times 325$.

Fig. 39. Longitudinal section of a two celled embryo. $\times 325$.

Fig. 40. Longitudinal section of a four celled embryo. $\times 325$.

Fig. 41. Longitudinal section of an eight celled embryo. $\times 325$.

Fig. 42. Not quite median longitudinal section of about a 20 celled embryo of the "filamentous" type. $\times 325$.

Fig. 43. Longitudinal section of an eight celled embryo of same type. $\times 325$.

Fig. 44. Transverse section near middle of a 30 celled embryo. $\times 325$.

Fig. 45. Longitudinal section of a 24-celled embryo of quadrant type. $\times 325$.

Fig. 46. Transverse section through the middle of a 52 celled embryo. Quadrant walls distinct. $\times 325$.

Fig. 47. Longitudinal section of an embryo of same type with capsule, stalk, and foot differentiating. $\times 325$.

Fig. 48. Longitudinal section of a later embryo showing sporogenous tissue distinctly. $\times 325$.

Fig. 49. Young androcyte showing diagonal cleavage between them. $\times 1600$.

Fig. 50. Androcyte after appearance of the blepharoplast. $\times 1600$.

Fig. 51. Blepharoplast near the nuclear wall. $\times 1600$.

Figs. 52, 53 and 54. Elongation of blepharoplast. $\times 1600$.

Figs. 55, 56 and 57. Elongation of nucleus. The blepharoplast has become associated with the nucleus. $\times 1600$.

Fig. 58. Distorted androcyte showing great elongation of blepharoplast. $\times 1600$.

Fig. 59. Further elongation of nucleus. $\times 1600$.

Figs. 60 and 61. Antherozoids from a dried smear. The anterior region is somewhat swollen. $\times 1600$.

PLATE 6.

Figs. 62, 63 and 64. Antherozoids from a dried smear. The anterior region is somewhat swollen. $\times 1600$.

Figs. 65, 66, 67, and 68. Young sporogenous tissue and elaters from various portions of the capsule. $\times 325$.

- Fig. 69. A portion of an elongated elater. $\times 325$.
- Figs. 70, 71, 72, and 73. First mitosis in a sporogenous cell that is to form a row of 8 spore mother cells. $\times 800$.
- Fig. 74. Several spore mother cell nuclei formed in such a sporogenous cell. The cross walls are not yet visible. $\times 325$.
- Fig. 75. Two of a row of spore mother cells increasing in size. $\times 325$.
- Figs. 76, 77, 78, 79, 80, and 81. Maturing of spore mother cells before meiosis. $\times 325$.
- Fig. 80. Terminal spore mother cell of a chain showing non-nucleate end of the parent sporogenous cell. $\times 325$.
- Fig. 82. Chain of spore mother cells in position as formed. $\times 325$.
- Figs. 83-97. Meiosis in spore mother cells.
- Fig. 83. The presynaptic spireme. $\times 1600$.
- Fig. 84. Synapsis. $\times 1600$.
- Fig. 85. Post-synaptic spireme. $\times 1600$.
- Fig. 86. Retreat of spireme to the nuclear wall. $\times 1600$.
- Fig. 87. Further retreat, paired chromomeres appearing. $\times 1600$.
- Fig. 88. Dyads formed. $\times 1600$.
- Fig. 89. Paired chromosomes on the heterotypic spindle. $\times 1600$.
- Fig. 90. Polar view of the heterotypic metaphasic plate. $\times 1600$.
- Fig. 91. Homeotypic prophase nucleus showing kinoplasm consisting of elliptical bodies after Gram's stain. $\times 1600$.
- Fig. 92. Metaphase of heterotypic division showing viscosity of chromosomes. Nine can be seen here. $\times 1600$.
- Fig. 93. Anaphase of heterotypic division. Ten chromosomes are present on both sides of the equator. One of the upper group lies under the others and is not drawn. $\times 1600$.
- Fig. 94. Formation of cell plate. Nuclei in prophase of homeotypic division. $\times 1600$.
- Fig. 95. Metaphasic plate of homeotypic division. Ten chromosomes appear in the figure. $\times 1600$.
- Fig. 96. Grouping of chromosomes in telophase of heterotypic division. $\times 1600$.
- Fig. 97. Elongation of daughter nuclei in preparation for homeotypic division. $\times 1600$.

PLATE 7

- Fig. 98. Metaphase of homeotypic division. Side and polar view of homeotypic spindles in same spore mother cell. $\times 1600$.
- Fig. 99. Three spores of a young tetrad. $\times 1600$.
- Fig. 100. Endosporium and exosporium formed, and episporium beginning to be formed. $\times 1600$.
- Fig. 101. Section through a mature spore. $\times 1600$.
- Fig. 102. a. A spore before enlargement has set in. $\times 170$. b-f. Stages in the rupture and dissolution of the spore coat of a germinating spore. First rhizoid appearing. These sporelings are two weeks old. $\times 170$.
- Fig. 103. 2-4 celled thalli $2\frac{1}{2}$ weeks old. The undigested papillate thickenings of the exospore are represented as irregularly scattered dashes. $\times 170$.

- Fig. 104 a-g. Initiation of the thallus. Thalli are four weeks old. g. Thallus showing ephemeral apical cell. $\times 85$.
Fig. 105. Thalli 5 and 6 weeks old showing the formation of the anterior marginal growing zone. $\times 85$.

PLATE 8

Unretouched photographs

- Figs. 106 and 107. Median sagittal sections of the thallus showing young male receptacles. $\times 47$.
Fig. 108. Longitudinal section of a young female receptacle. $\times 47$.
Figs. 109, 110, and 111. Developmental stages of the sporophyte in longitudinal sections. The foot and seta are often wider than in fig. 111. $\times 47$.
Fig. 112. Annular thickenings in the cells of the capsular wall. $\times 170$.
Fig. 113. Zone of contact of foot of sporogonium with the floor of the archegonium. Cells of seta are divided in preparation for elongation. $\times 170$.
Fig. 114. Spore tetrads and elaters. $\times 170$.
Fig. 115. Peg rhizoids from a furrow of the female receptacle showing copious mucilage unbleached from osmic blackening. $\times 170$.
Fig. 116. Similar section to figure 115 after bleaching and staining. $\times 170$.
Fig. 117. Three mucilaginous cells in a section of the involucre. $\times 170$.

PLATE 4

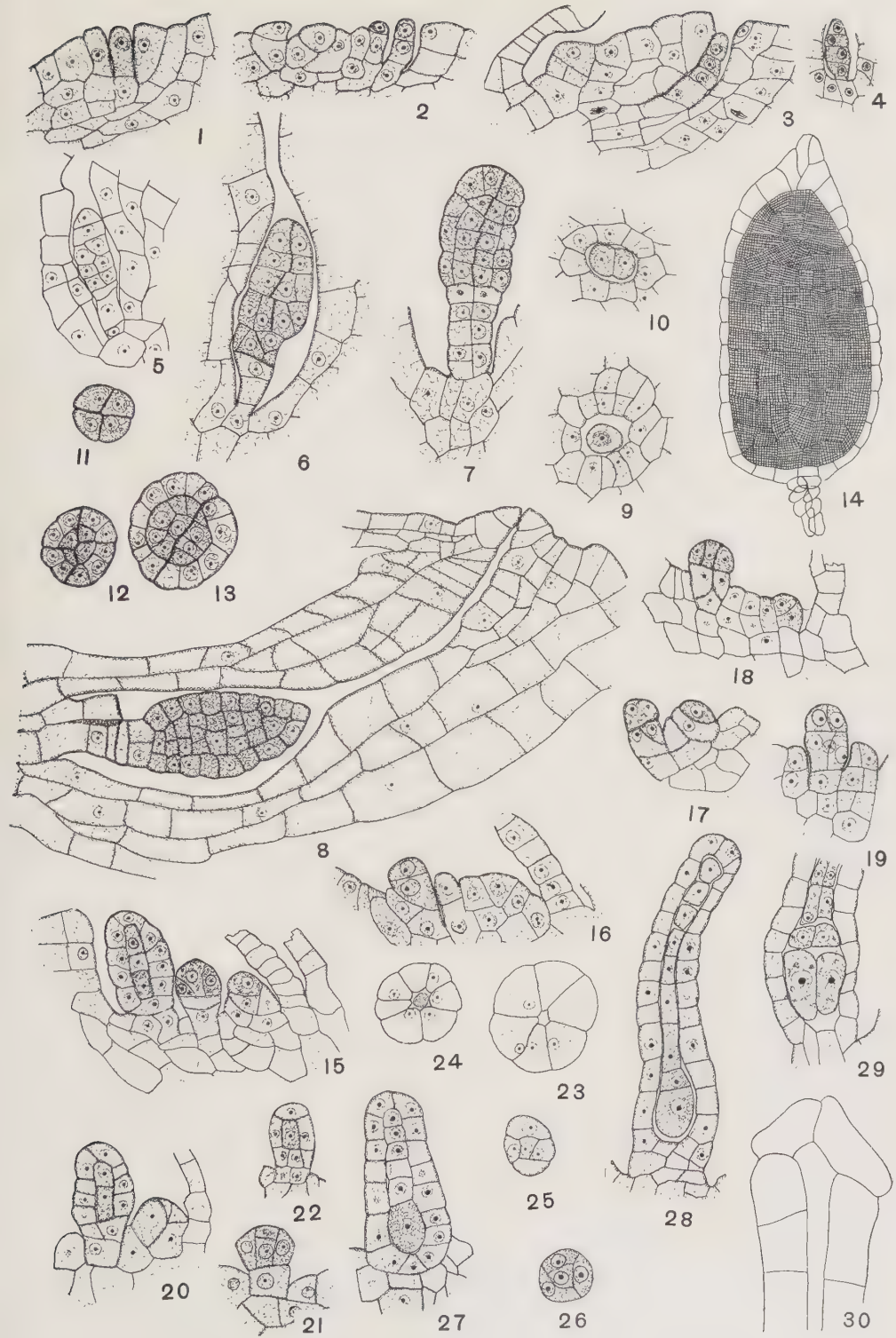


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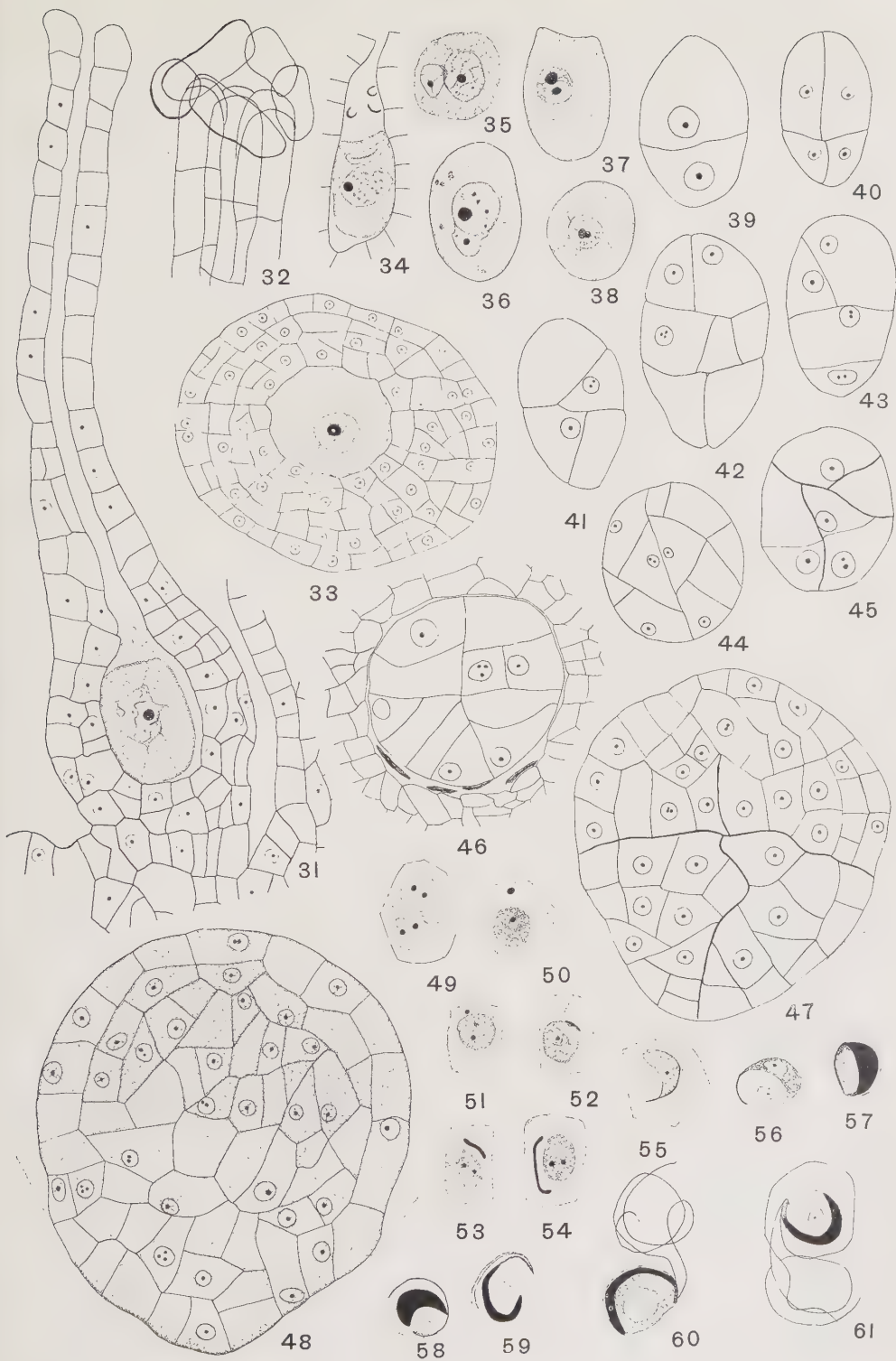


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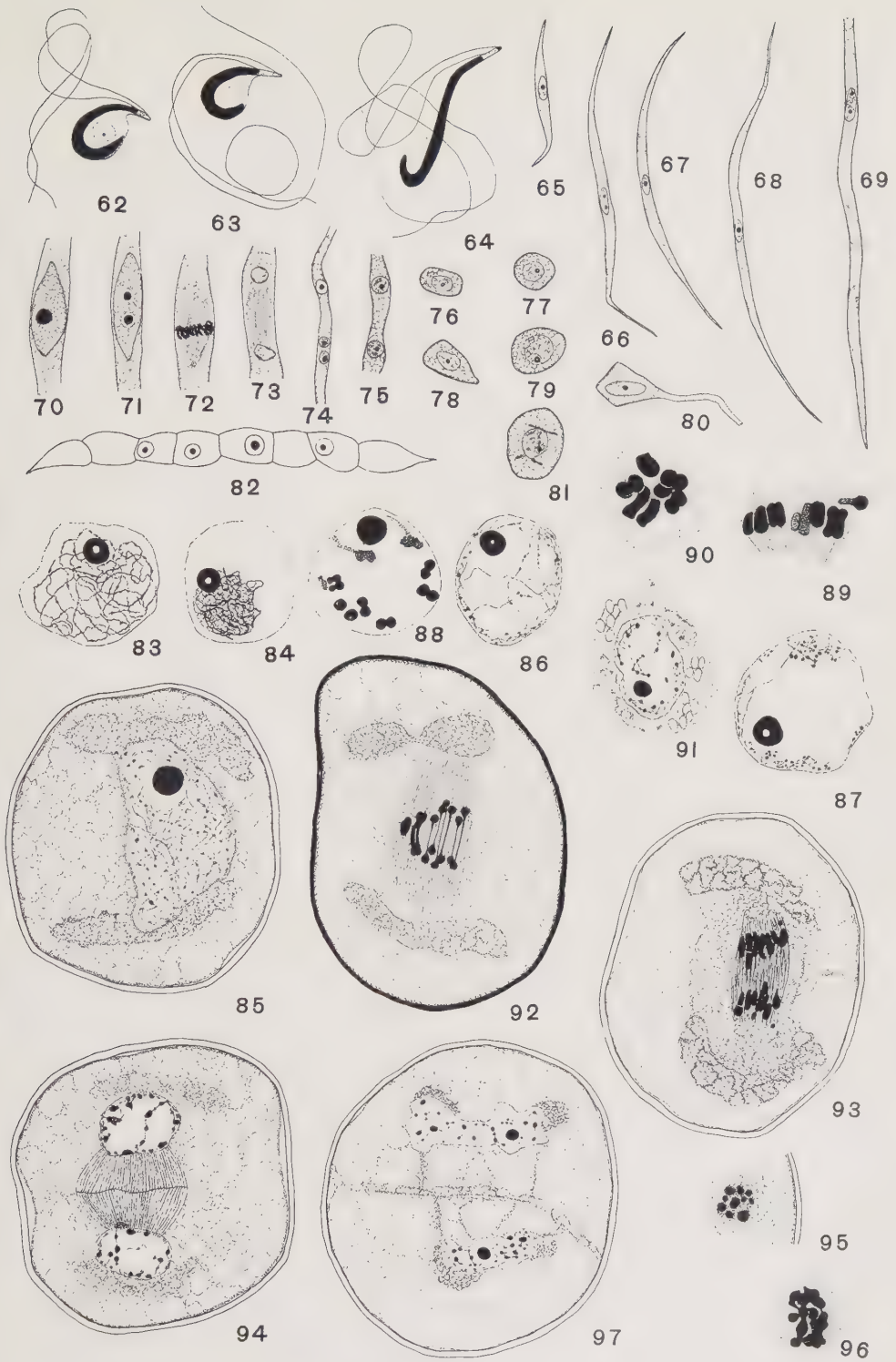
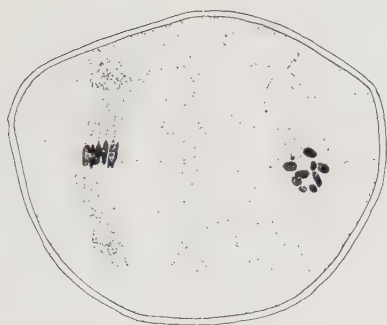


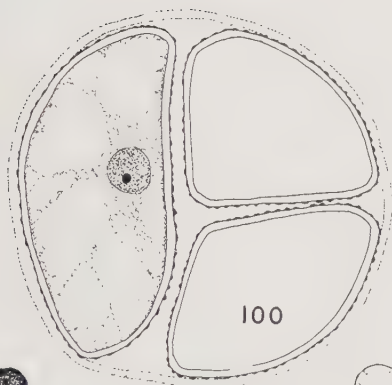
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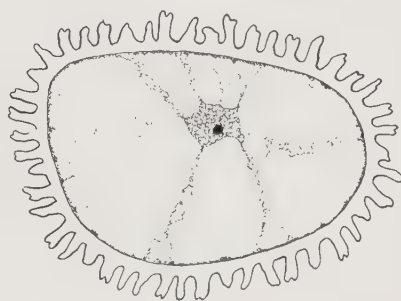
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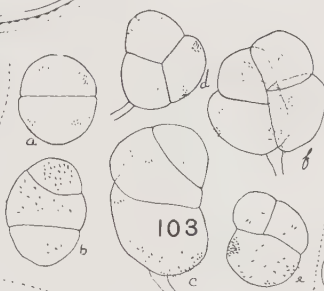
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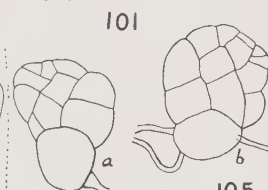
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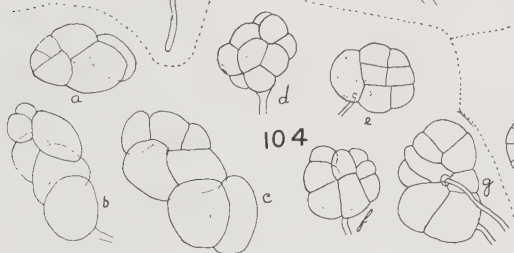
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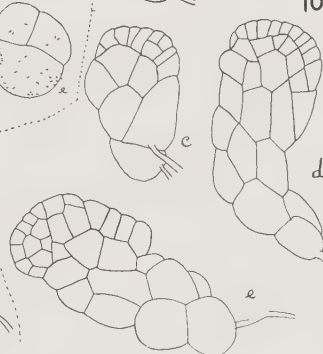
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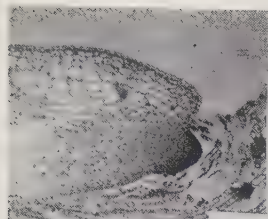


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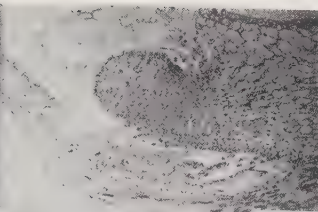
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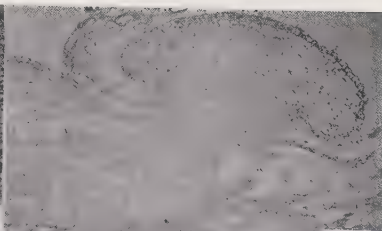
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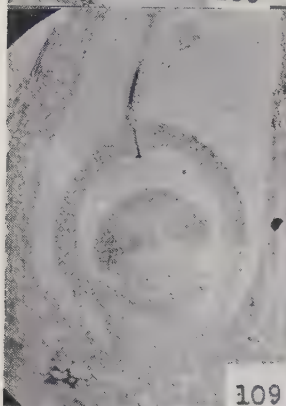
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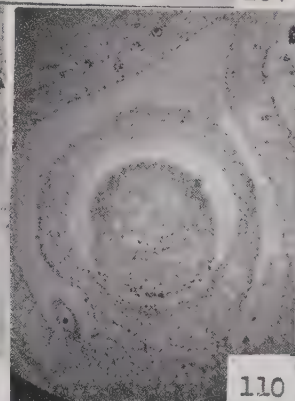
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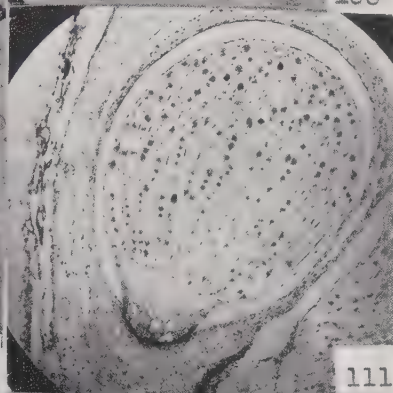
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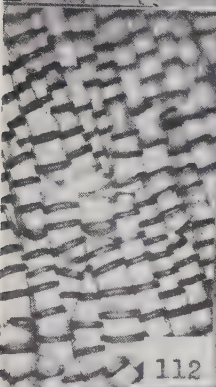
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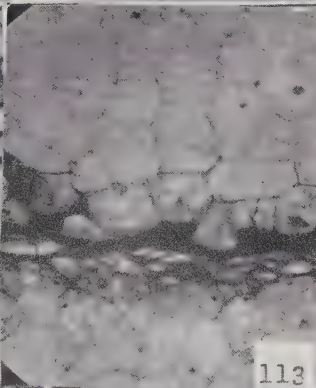
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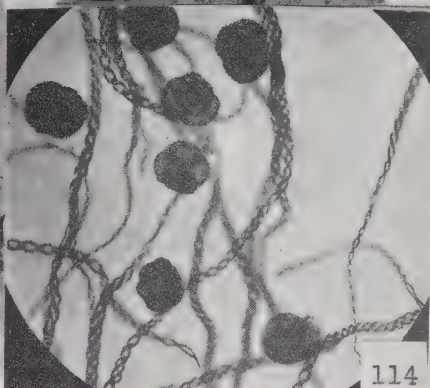
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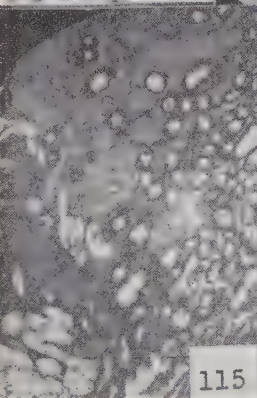
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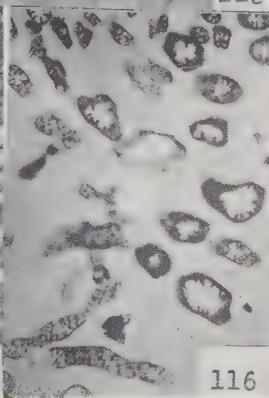
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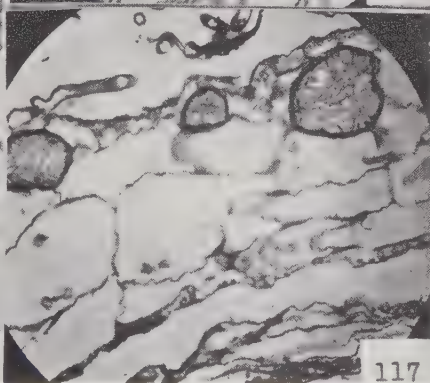
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VITA

Paul Morrison Patterson, son of Dr. and Mrs. B. C. Patterson, missionaries to China under the Southern Presbyterian Mission Board, was born February 25, 1902, in Sutsien, Kiangsu, China. Grammar school education was taken at home, the first two years of high school at Shanghai American School, later finishing at Lexington High School, Lexington, Va., in 1921. An A.B. degree was taken at Davidson College in 1925, and an A.M. in botany, at the University of North Carolina in 1927. During 1926-'27 he was part-time instructor in botany at the University of North Carolina, and an assistant professor of biology at Davidson College in 1927-'28. Further graduate work was taken in botany at the Johns Hopkins University during 1928-'30. In connection with this, three summers were spent in botanical work: one at Mt. Desert Island, Maine; a second in Baltimore and a third in Jamaica, B. W. I. He became associate professor of biology at the University of South Carolina in 1930, completing his requirements for the degree of doctor of philosophy in botany at the Johns Hopkins University during a leave of absence from the latter university in 1932-'33.

